What are the fundamental questions regarding evolution in ecological networks?

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Accepted for publication by *Trends in Ecology and Evolution* on 12 Jun 2020
https://doi.org/10.1016/j.tree.2020.06.004

Reviewing *The Role of Evolution in Shaping Ecological Networks*, Segar *et al.* [1] stirred controversy over the central question [2]. I propose to settle this by defining concepts more clearly; answer other "Outstanding Questions" raised by Segar *et al.* [1]; and draw attention to some very different related open fundamental questions.

Clarification of concepts

Adjacency matrices of ecological networks are thresholded matrices of interaction strengths [3, 4]. Denote for any two species i, j by A_{ij} the strength of the directed interaction (of a particular type) between them, defined such that these values are robust to variation in the abundance of i, j and other species—e.g. for trophic interactions as the attack-rate parameter in a fitted functional response [5]. The idea that "patterns in networks are mediated by species-specific traits" [1] has been formalised [4] by the condition that there is a function $\tilde{a}$ such that

$$A_{ij} = \tilde{a}(\mathbf{t}_i, \mathbf{t}_j), \tag{1}$$

where, for any species k, the vector $\mathbf{t}_k$ provides quantitative characterisations of all its ecologically relevant traits.

The idea of traits specific to particular ecological roles, e.g. "consumer traits" [1], has been formalised

[4] by the condition that there are continuous functions V and F mapping trait vectors $\mathbf{t}$ into lower-dimensional trait spaces such that, for some continuous function a,

$$A_{ij} \approx a\big(V(\mathbf{t}_i), F(\mathbf{t}_j)\big). \tag{2}$$

Defining for any species k its *vulnerability traits* as $\mathbf{v}_k = V(\mathbf{t}_k)$ and its *foraging traits* as $\mathbf{f}_k = F(\mathbf{t}_k)$,

$$A_{ij} \approx a\big(\mathbf{v}_i, \mathbf{f}_j\big). \tag{3}$$

Network evolution must be modelled through the evolution of these traits—which answers the second "Outstanding Questions" of [1]. Modelling the A_{ij} directly as "evolving traits" [1] leads to artefacts [6].

The idea of trait "matching" [1, 6] between interaction partners such as consumers and resources is captured by generic models for the function a such as [4]

$$a(\mathbf{v}, \mathbf{f}) = a_0 \exp\left[v_0 + f_0 - \frac{1}{2}\sum_{k=1}^{D} \sigma_k (v_k - f_k)^2\right], \tag{4}$$

with D denoting the dimensionality of trophic niche space and $v_0, \ldots, v_D$ and $f_0, \ldots, f_D$ the components of $\mathbf{v}$ and $\mathbf{f}$, respectively. The constant a_0 has the appropriate dimensions and $\sigma_k = \pm 1$ [4]. When imposing a condition that the sum of v_0^2 over all species is minimised, $\mathbf{f}$- and $\mathbf{v}$-vectors are uniquely determined up to rigid geometric transformations, thus *reproducibly characterising species rather than data sets* [4]. In this setting, a perfect "match" means equality of all but the first components of $\mathbf{v}$ and $\mathbf{f}$ [4].

Equation (4) can be expressed in the equivalent form [6, 7]

$$a(\mathbf{v}, \mathbf{f}) = \hat{a}(\hat{v}_0, \hat{\mathbf{v}}, \hat{f}_0, \hat{\mathbf{f}}) = a_0 \exp\left[\hat{v}_0 + \hat{f}_0 + \hat{\mathbf{v}} \cdot \hat{\mathbf{f}}\right], \tag{5}$$

with the number $\hat{v}_0$ and the D-component vector $\hat{\mathbf{v}}$ given by $\mathbf{v}$, and $\hat{f}_0$, $\hat{\mathbf{f}}$ given by $\mathbf{f}$ [4]. Both formulations, Eqs. (4) and (5), have been empirically verified for food webs [4, 7], but are applicable more widely.

Resolution of a controversy

Segar et al. [1] and Sagoff [2] differ over whether "The structure of ecological networks reflects the evolutionary history of their biotic components." As a general statement, this is correct in two different but weak senses. First, because, at the fundamental level, ecological interactions, ecology and evolution are inseparable [10]. Second, in terms of phylogenetic signal.

By Eq. (3), phylogenetic signal arises in networks if there is phylogenetic signal in the $\mathbf{v}$-traits or the

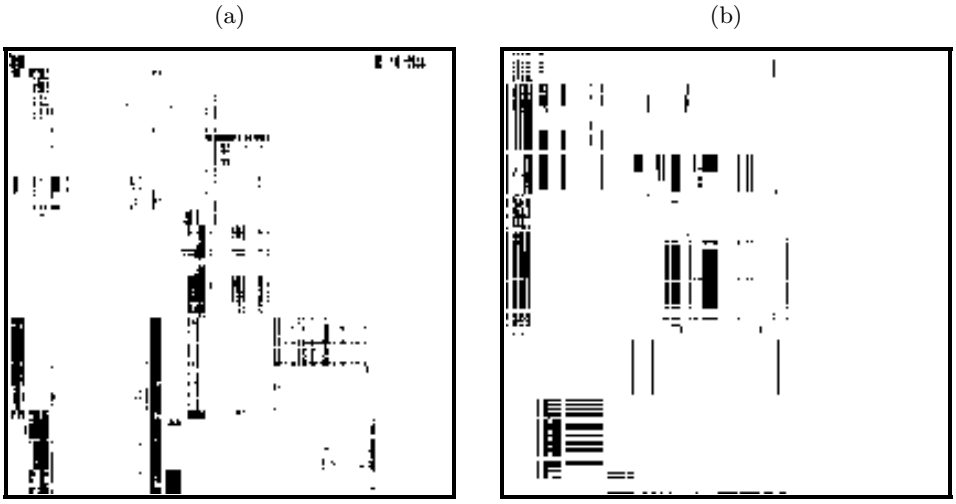

Figure 1: **Phylogenetic signal in the adjacency matrix of a model food web compared to empirical data.** Black pixels denote trophic links. Rows correspond to species as resources, columns to species as consumers; the ordering of species is identical along rows and columns and such that related species are grouped together. Panel (a) is a random sample from the Matching Model [6], which employs a link-strength function equivalent to Eq. (5) with fixed $\hat{v}_0$, $\hat{f}_0 = 0$ and neutrally evolving, phylogenetically correlated vulnerability- and foraging trait vectors $\hat{\mathbf{v}}$, $\hat{\mathbf{f}}$. In panel (a) $\hat{\mathbf{v}}$-traits evolve slower than $\hat{\mathbf{f}}$-traits [6], implying that related species tend to have more similar sets of consumers than sets of resources [8], as apparent from the vertically stretched structures. There is no selection, no correlation between $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ traits, and hence no tracking or co-evolution. Structures seen in panel (a) are due to phylogenetic signal alone. Panel (b) represents the food web of Little-Rock Lake as reported in [9]. Modified with permission from [4].

f-traits, but not necessarily in both, as Segar et al. appear to suggest. In food webs, for example, **v**-traits evolve much slower than **f**-traits, leading to stronger phylogenetic signal [6, 8] (Fig. 1). This, combined with a large-eats-small rule, is sufficient to produce food webs with highly realistic network properties [4, 6] (answering the fifth "Outstanding Questions" of [1]). Thus, network structure reflects evolutionary history: some birds feed on insects, others on weeds, yet most birds could fall prey to peregrine falcons. It's common knowledge.

More interesting, though, is the question under which conditions evolutionary change in the **v**-traits of taxa gets into lockstep with **f**-traits of closely matching taxa. Plausibly, this requires frequent co-occurrence of the two taxa. Because, as Sagoff [2] explains, such close associations are for species rather the exception than the rule, so should be these co-evolution or tracking phenomena. Instead, community turnover through space and time generates ever-changing *fitness seascapes* [11], driving random-walk evolution of **v**- and **f**-traits. Correspondingly, pairwise link-strength distributions are consistent with random expectation [3].

Transitions between tracking and losing track of close interaction partners are empirically well described [12]. However, reliance on network modularity (block structure in adjacency matrices) as evidence for cases of tracking or co-evolution [1] risks overestimating their prevalence. Uncorrelated phylogenetic signals in **v**- and **f**-traits already generate such patterns [4, 6] (Fig. 1).

Unanswered fundamental questions

A fundamental question arising from these considerations is why, despite phylogeny being so deeply imprinted in network structure, it appears of little relevance for explaining high-level ecological phenomena. The Population Dynamical Matching Model, for example, which combines phylogenetically structured assembly with coevolutionary feedbacks through direct and indirect trophic interactions, is highly successful in reproducing not only network structure [13] and but also macroecological characteristics [4, 13, 14] of observed communities (thus answering the first "Outstanding Questions" of [1]). Yet, the mathematical explanations of these characteristics [4] scarcely draw on the phylogenetic structure.

This is not to say that evolution can ultimately be disregarded. For example, there is evidence for network-level selection of key parameters such as baseline foraging traits f_0 [4, 13], dietary diversity [3, 4], and predator-prey mass ratios [15]. One should therefore ask: does this mean that consumer behaviour and body plans are fundamentally determined at the ecosystem level?

Acknowledgements

This work was supported by the Natural Environment Research Council (NE/T003510/1).

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